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Seasonal Photosynthesis and Partitioning of Nonstructural Carbohydrates in Leafy Spurge (*Euphorbia esula*)

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Previous evidence indicates that changes in well-defined phases of dormancy in underground adventitious buds of leafy spurge in late summer and autumn are regulated by complex sensing and signaling pathways involving aboveground sugar signals. However, little information exists concerning seasonal photosynthesis and carbohydrate partitioning of leafy spurge, although such information would help to elucidate the involvement of sugar in controlling bud dormancy. An outdoor study was conducted over two growing seasons to determine and model seasonal patterns of photosynthesis and aboveground carbohydrate partitioning and their relationship to underground adventitious bud carbohydrate status. Photosynthesis and total nonstructural carbohydrate (TNC) content of aboveground tissues was greatest during vegetative growth. Photosynthesis gradually declined over the growing season, whereas TNC decreased sharply during flowering, followed by a gradual decline between midsummer and autumn. Leaf starch increased dramatically to midsummer before declining sharply throughout late summer and early autumn, whereas sucrose content responded inversely, indicating a mobilization of starch reserves and export of sugars to overwintering belowground sink tissues. Because newly formed underground adventitious buds showed a continuous increase in TNC from midsummer through autumn, export of sugars from aboveground tissues likely contributed to the increase in TNC. These results may facilitate new strategies for biological control of leafy spurge.

Nomenclature: Leafy spurge, *Euphorbia esula* L.
Key words: Carbohydrate partitioning, dormancy, photosynthesis.

Leafy spurge is an invasive perennial weed causing economic losses to range, recreational, and right-of-way lands in North American plains and prairies (Bangsund et al. 1999; Leitch et al. 1996). Its perennial nature is primarily attributed to vegetative propagation via new shoot growth from an abundance of underground adventitious buds found on its crown and extensive root system (Morrow 1979). New underground adventitious buds develop on the crown and roots from early to mid-summer, but they are inhibited from initiating new shoot growth by mechanisms regulating the well-defined phases of seasonal dormancy (para-, endo-, and ecodormancy) until the following spring (Anderson et al. 2005). Dormancy-imposed inhibition of new shoot growth from underground adventitious buds is one of the key characteristics leading to the persistence of perennial weeds such as leafy spurge (Coupland et al. 1955). As a result, dormancy facilitates the distribution of shoot emergence over time and is, therefore, a critical factor that allows weeds to escape control by chemical, cultural, mechanical, and biological control measures (Anderson et al. 2001; CAB 2004).

Dormancy in underground adventitious buds of leafy spurge can be affected by factors such as phytohormones, water, and nutrient status (Harvey and Nowierski 1988; Horvath 1999; McIntyre 1972, 1979; Nissen and Foley 1987) and gibberellic acid (GA) has long been known to break dormancy (Horvath 1999; Horvath et al. 2002; Shafer and Monson 1958). Additional research has demonstrated that basipetal auxin transport from shoot apices (Horvath 1998) and a leaf-derived signal that requires photosynthesis (Horvath 1999; Horvath et al. 2002) are primarily responsible for maintaining paradormancy (also referred to as apical dominance or correlative inhibition) in underground adventitious buds of leafy spurge. The leaf-derived signal required for maintaining paradormancy may involve a sugar-sensing pathway (Anderson et al. 2005, Horvath et al. 2002). Indeed, as little as 30 mM sucrose or glucose can inhibit underground adventitious bud growth through a mechanism reversible by GA (Chao et al. 2006).

As the foliar tissue of leafy spurge senesces during autumn, underground adventitious buds transition from a state of paradormancy to endodormancy, which is maintained until sustained low temperatures cause a transition from endodormancy to ecodormancy (Anderson et al. 2005). Establishment and maintenance of endodormancy is critical for bridging the gap between the well-defined phases of para- and ecodormancy, a period when the environmental conditions of autumn still can be conducive for induction of new shoot growth. During the transition into endodormancy, there is a paralleled decrease in starch levels in underground adventitious buds and an increase in soluble sucrose (Anderson et al. 2005). In contrast, induction of new shoot growth by removing the signaling mechanisms regulating paradormancy in underground adventitious buds results in a reduction of both endogenous starch and sucrose but an increase in soluble fructose (Chao et al. 2006).

Models developed based on available data and literature indicate that sugar-signaling may play a significant role in regulating growth and development in underground adventitious buds of leafy spurge during well-defined phases of dormancy (Anderson et al. 2005; Horvath et al. 2003). However, there are few published studies that have focused on photosynthetic processes in leafy spurge and none that we are aware of that address seasonal photosynthesis and aboveground carbohydrate partitioning. Incorporating better knowledge of these processes into our present understanding of the regulation of bud dormancy will assist in devising integrated management strategies for leafy spurge. A 2-yr field study was conducted to provide a clearer understanding of seasonal trends in leaf photosynthesis and aboveground carbohydrate partitioning and how these processes relate to root bud carbohydrate levels, which may influence their growth and dormancy.

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Materials and Methods

Plant Material. This study was conducted in 2002 and 2003 at a field site in Morris, MN (45°34′38″N, 95°54′36″E). Plants of leafy spurge Biotype 1984-ND001 were grown in 0.20-m-diam by 0.41-m-long cylindrical pots filled with a sandy loam soil without added fertilizer. Plants were originally propagated from shoot cuttings (2 cuttings per pot) in 2000 and grown in Fargo, ND (46°53′60″N, 96°47′60″E) (Anderson et al. 2005) before a group of potted plants were transferred to the Morris, MN, site in early April 2002. The cylinders containing plants were housed inside polyvinyl chloride (PVC) sleeves that were buried in the soil, so that only 0.05 m of the pots protruded above the soil surface. The pots were grouped into three replicated blocks that were 0.6-m wide by 5.5-m long. Each block was subdivided into five groups of four pots. Air temperature and precipitation were collected at a weather station approximately 3.2 km from the study site.

Plant Sampling and Photosynthesis. Leafy spurge plants were sampled at approximately 4-wk intervals during the growing season from mid-May to late October. At each interval, three randomly chosen plants, each from a different group of pots within a block, were sampled from each replicated block. The plants were cut at the base of the soil and brought back to a nearby lab where they were quickly separated into stems and leaves. Tissue dry weights were recorded per plant after drying in a forced air oven for a minimum of 48 h at 65 C. Dry stem and leaf material were pooled separately for each replicated block of plants and ground to a fine powder in a Wiley mill and stored dry for carbohydrate analysis.

Newly forming adventitious root buds were sampled during the growing season of 2002 and 2003 from plants grown outdoors at Fargo, ND (175 km from the Morris site), using the same experimental system as the Morris, MN, site (plants were the same age). At 2 to 4-wk intervals, the root systems of two randomly chosen plants were excavated and newly formed buds on crown tissue were extracted and stored at −80 C until analyzed for carbohydrates. Before carbohydrate analysis, bud tissue was ground to a fine powder in liquid nitrogen.

Leaf photosynthesis was measured on intact plants at the field site using a LI-6400 Portable Photosynthesis System[1] between 10:30 and 11:30 A.M. Central Standard Time. Measurements were made at ambient air temperature on sun-exposed, uppermost, fully expanded leaflets under a CO_2 concentration of 400 μmol mol^{-1} and 1,500 μmol m^{-2} s^{-1} of photosynthetically active radiation using an artificial light source. Leaves for three to six separate randomly chosen plants from each replicated block were measured at each sampling interval.

Carbohydrate Analysis. Tissue extraction and carbohydrate analysis was done as previously described by Anderson et al. (2005). Approximately 150 mg of ground, dried plant material, or 250 mg of ground, fresh bud material was extracted three to four times in 4 ml of 80% (vol/vol) ethanol at 85 C. The extracts were combined for each sample, and all samples were brought up to the same volume before adding 200 mg of activated charcoal to clarify the solutions overnight at 4 C. The samples were then evaporated overnight at 60 C, resuspended in 2 ml of deionized H_2O and filtered (0.45 μm).[2] Glucose, fructose, and sucrose were determined by high-performance liquid chromatography[3] using an Aminex HPX-87N column[4] and refractive index detector at a flow rate of 0.5 ml min^{-1} in 0.01 M Na_2–HPO_4.

The pellet remaining after ethanol extraction was dried at 60 C and used for determining starch. Pellets were incubated in 1 ml of 0.2 N KOH in boiling H_2O for 30 min. After cooling, 0.2 ml of 1 N acetic acid was added, and the solution was incubated with 2 ml of acetate buffer (pH 4.6) containing 6 units of amyloglucosidase[6] at 55 C for 1 h with agitation. The reaction was terminated in a boiling water bath. After centrifuging at 3,500 × g for 1 min, the resulting supernatant was dried at 60 C, resuspended in 2 ml deionized H_2O, filtered $(0.45\ \mu m)^2$, and assayed for glucose. Starch measurements are reported as glucose equivalents. Total nonstructural carbohydrate (TNC) was calculated as the sum of glucose, fructose, sucrose, and starch. The carbohydrate extraction and measurement procedures were performed three separate times for each tissue sample.

Statistics. All data were plotted as a function of time and weighted least squares regression was used to analyze the relationship. Analyses were performed using TableCurve 2D[6] and SAS PC Windows.[7] Equations for each year were developed using the means of the dependent variable at each Julian date weighted by 1/variance in weighted least-squares regression analysis. Full and reduced models were compared to determine whether there were significant differences between equations (i.e., years) at $P \leq 0.05$. If overall differences were detected between the equations for each year, indicator variable analysis was used to determine which regression coefficients were responsible for the difference. Because of the nature of the response, particularly in 2002, two separate equations for each year were used to model total aboveground and stem nonstructural carbohydrate content. The first model described the response between May and early July and the second was used to describe the response between late July and late October.

Results and Discussion

Leafy spurge shoots generally began to emerge from the soil in mid to late April during the study. Leaf photosynthesis was greatest during vegetative growth of plants in May (Figure 1). Although photosynthesis decreased 14 to 24% in June, when plants began flowering, it remained relatively steady through late July before declining again throughout late summer and autumn. Photosynthesis was significantly affected by growing season ($P < 0.05$) and was generally greater in 2002 than 2003 ($P = 0.01$). However, the trend was similar for both years.

New leafy spurge shoot growth arises from underground adventitious buds formed during the previous growing season (Anderson et al. 2005), which appears to coincide with long photoperiods. In the present study, photosynthesis was greatest just before the longest photoperiod of the year (Figure 1). If indeed sugar is the leaf-derived signal for controlling paradormancy in underground adventitious buds (Anderson et al. 2005; Chao et al. 2006; Horvath et al. 2002), then high photosynthetic rates during the spring and summer

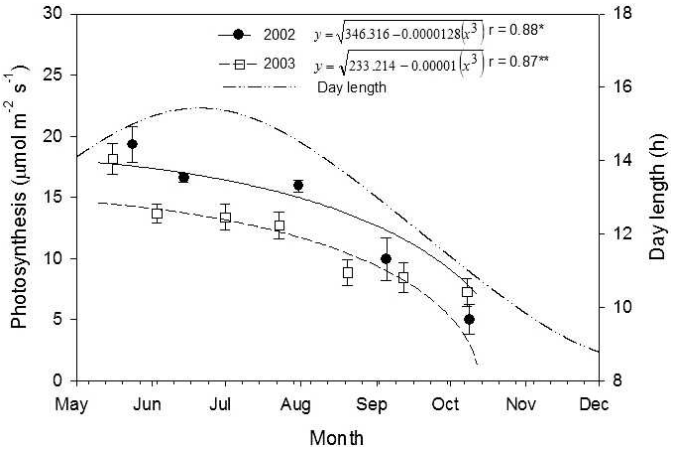

Figure 1. Seasonal influence on leaf photosynthesis and photoperiod. Photosynthesis values are means ± SE, n = 9 to 18. Photoperiod is for Morris, MN (45°34′38′′N, 95°54′36′′E). Significance is at * P ≤ 0.05 and ** P ≤ 0.01 levels, respectively.

(May through July) are vital in providing carbohydrates for both growth and maintenance of aboveground tissues as well as developmental processes in underground adventitious buds.

As with photosynthesis, TNC in aboveground tissues was greatest early in the growing season and generally declined as the season progressed (Figure 2A). Between May and early July there was a sharp (40%) decline in TNC. This may have been partly due to demand for photo-assimilate associated with flowering and seed set of plants, but also was likely related to partitioning of carbohydrates to roots. Lym and Messersmith (1987) measured TNC in leafy spurge roots from early April through late October. They found that TNC concentration was lowest in early spring (April) and increased dramatically between May and early to mid-July, and although levels modulated during late summer, they remained considerably higher than during the early growing season. Furthermore, the translocation of aboveground applied picloram to the roots of leafy spurge has been shown to be greatest during the period of flowering and seed set (Lym and Messersmith 1991).

From late July through early October the decline in aboveground TNC tended to be more gradual before sharply declining in late October as aboveground tissues senesced with the onset of autumn (Figure 2A). Flowering and seed set of leafy spurge were completed by late July. Thus, the more gradual decline in TNC from late July through early October may have been related to these processes no longer being an active sink for photoassimilate. As with the sharp decrease observed in the early growing season, the decline in late October is likely due to translocation of carbohydrates to belowground reserves. In this regard, leafy spurge may be similar to Canada thistle [*Cirsium arvense* (L.) Scop.], another noxious perennial weed that vegetatively propagates from roots. Canada thistle shows marked increases in the translocation of assimilated ^{14}C to roots during spring growth leading up to flowering and again in the autumn (Tworkoski 1992). In the present study, total aboveground TNC was significantly affected by season (P ≤ 0.05), and the response was different between years (P = 0.01) for the period of late July through October but not between May and early July.

The overall higher TNC concentrations as well as photosynthesis during 2002 were probably related to plant

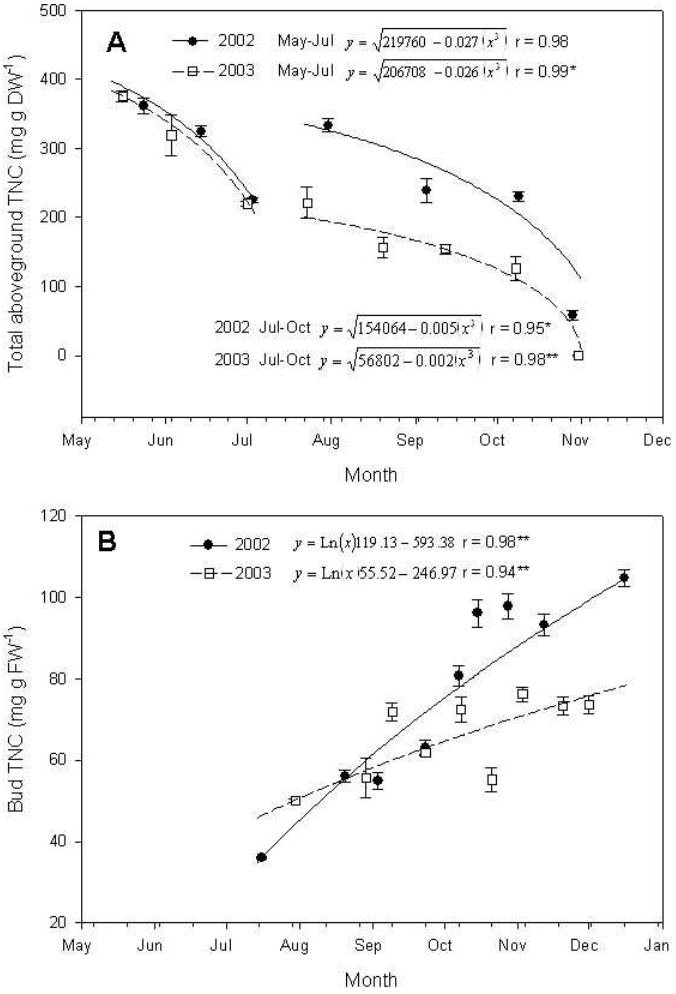

Figure 2. Seasonal influence on total (A) aboveground and (B) underground adventitious bud total nonstructural carbohydrate (TNC) content. Values are means ± SE, n = 3. Significance is at * P ≤ 0.05 and ** P ≤ 0.01 levels, respectively.

age and soil nutrition. Over four growing seasons, Lym and Messersmith (1987) found that leafy spurge root TNC gradually declined from one season to the next. In their study, the cause of the decline was not clear although factors such as dilution due to a larger root system, reduced soil nutrition, and decreased plant vigor with age were cited as possibilities. Although not measured in the present study, the amount of available soil nutrients was likely less in 2003 as plants were left undisturbed and not fertilized. Also, spurge plants may have become less vigorous with age. Cumulative precipitation during the 2002 and 2003 growing seasons (i.e., May through October) was 518 and 513 mm, respectively, and the mean air temperature was 16.1 and 16.9 C, respectively. Therefore, climate factors probably did not influence overall differences between years as greatly as did plant age and soil nutrition.

New underground adventitious buds on plants grown in Fargo typically began to be visible from late May to early June (Anderson et al. 2005). The TNC content in these buds was inversely related to that of aboveground tissues, tending to increase linearly from July through late autumn (Figure 2B). The increase of bud TNC during 2003 was not as great as that in 2002. Again, this may have been due to increase in plant age and reduced soil nutrition as cited for total aboveground TNC. Alternatively, the lower bud TNC during 2003, which

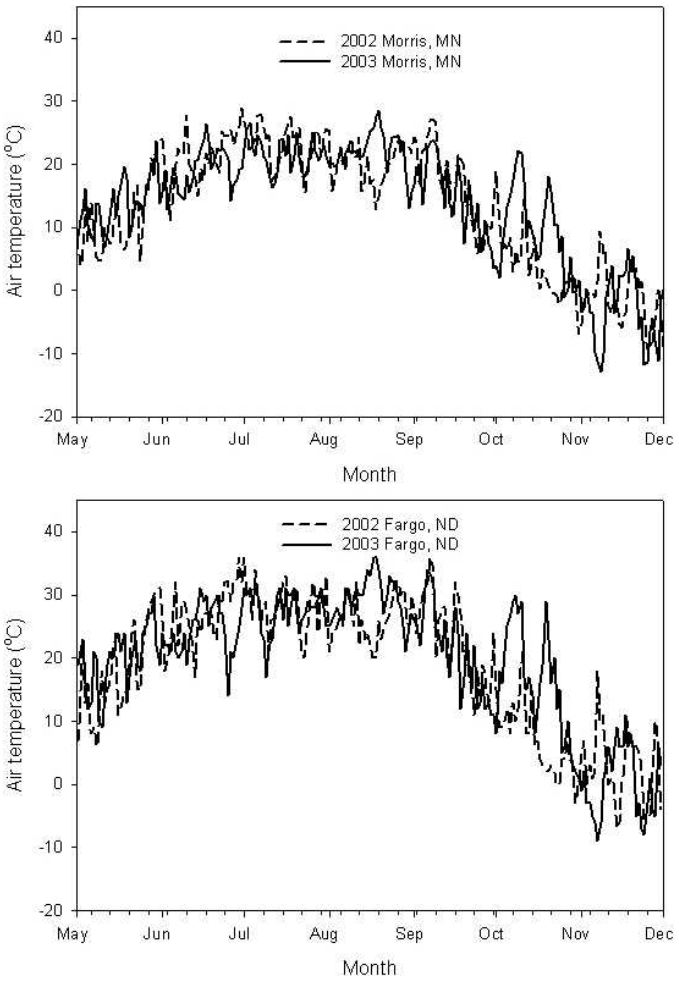

Figure 3. Seasonal daily average air temperature measured during 2002 and 2003 at Morris, MN, and Fargo, ND.

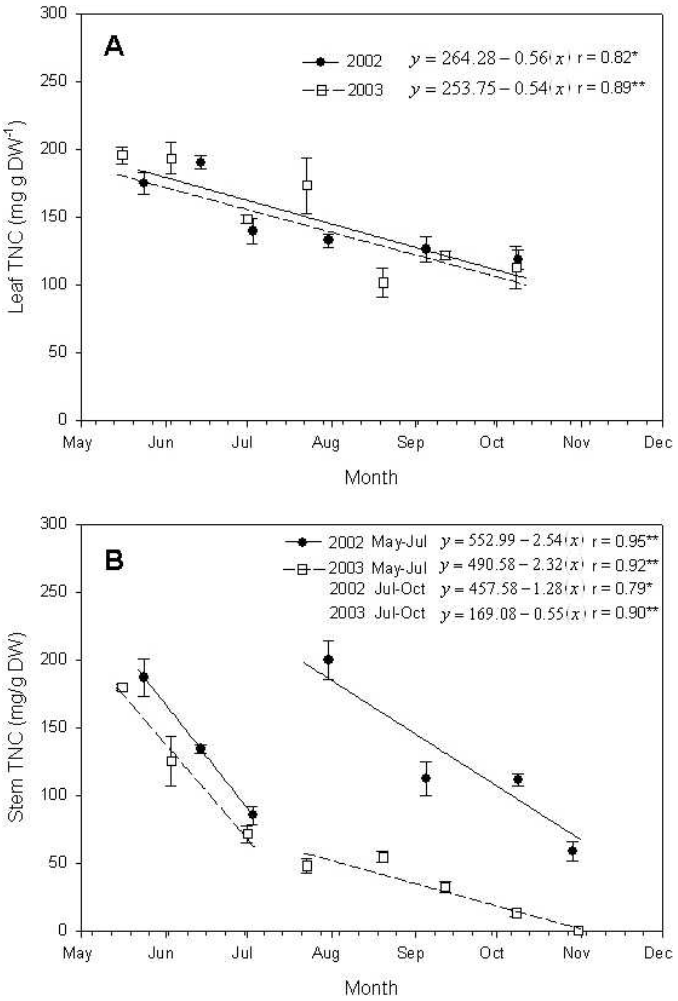

Figure 4. Seasonal influence on (A) leaf and (B) stem total nonstructural carbohydrate content (TNC). Values are means ± SE, $n = 3$. Significance is at * $P \leq 0.05$ and ** $P \leq 0.01$ levels, respectively.

was most prevalent in autumn could have resulted from higher autumn temperatures causing greater use of carbohydrates in respiration. In particular, the average temperature for the month of October in 2003 was 9 and 6 C greater than that in 2002 for Fargo and Morris, respectively (Figure 3). Furthermore, lower photosynthesis and aboveground TNC in 2003 (Figures 1 and 2A), as compared with 2002, may have resulted in less carbohydrate being partitioned to roots. It is known that excess photosynthate is stored as nonstructural carbohydrate in perennating organs of temperate weed species as an overwintering strategy (Cyr and Bewley 1989). Additionally, Figure 3 shows that although air temperature recorded at Fargo tended to be slightly higher than that at Morris, the patterns were quite similar at the two locations during both years of the study.

The TNC contents in leaves and stems were influenced significantly ($P \leq 0.05$) by season (Figure 4). The response of leaf TNC as a function of season (Figure 4A) was not different between years, but it was for stem TNC (Figure 4B; $P \leq 0.05$). During May of both years, the amount of nonstructural carbohydrate in leaves was about equal to that in stems. For the remainder of the growing season, in 2002, leaf TNC was 40 to 64% greater than that in stems in June and early July, 34% lower at the beginning of August and nearly equal to stems again in September and October. Between July and October of 2003, TNC content of leaves was from 1.5- to 8.5-fold greater than that in stems. The data indicate that in 2002 carbohydrate sink capacity, averaged across the growing season, was similar for both stems and leaves. In 2003, carbohydrate sink capacity was similar for leaves and stems at the beginning of the season (i.e., May) but was considerably greater for leaves from June through October.

We found that TNC of leafy spurge leaves and stems was composed mainly of sucrose and starch, similar to the finding of others for above and belowground tissues (Anderson et al. 2005; Le Tourneau 1956; Lym and Messersmith 1987). However, hexose sugar (glucose and fructose) content was relatively high during the early growing season in May and June, averaging 74 and 107 mg g^{-1} dry weight for leaves and stems, respectively (data not shown). Hexose content then dramatically decreased in July and remained low throughout the rest of the growing season averaging only 26 and 20 mg g^{-1} dry weight in leaves and stems, respectively.

Leaf starch and sucrose content were affected by season ($P \leq 0.05$) and tended to vary inversely to one another (Figures 5A and B). Although stem starch content responded similar to that in leaves and was affected by season ($P \leq 0.05$), there was no clear pattern for stem sucrose, which tended to fluctuate throughout the season (Figures 5C and D). From

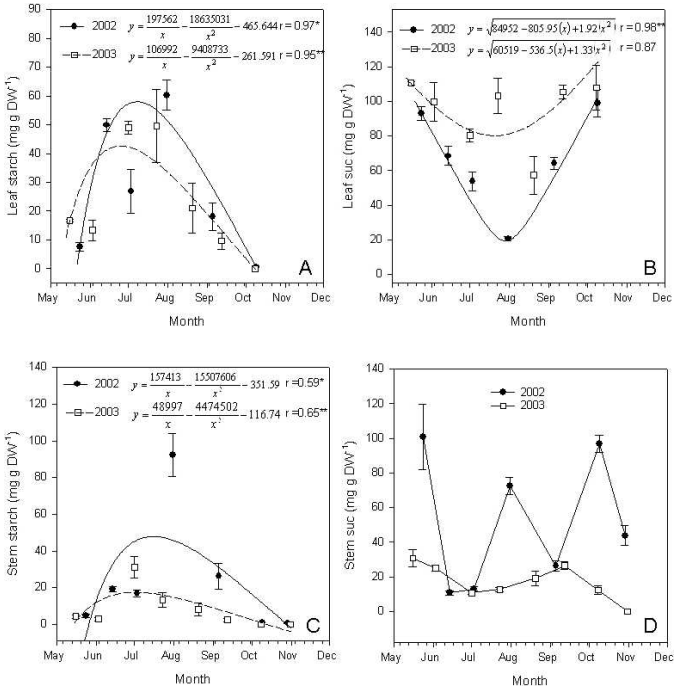

Figure 5. Seasonal influence on (A) leaf starch and (B) sucrose, and (C) stem starch and (D) sucrose content. Values are means ± SE, $n = 3$. Significance is at * $P \leq 0.05$ and ** $P \leq 0.01$ levels, respectively.

May to mid-summer, leaves accumulated starch while sucrose greatly declined. Conversely, as photosynthetic capacity declined from late summer through autumn (Figure 1), starch dramatically decreased with a concomitant increase in sucrose to levels similar to that at the beginning of the season (Figures 5A and B). Thus, as reduced photosynthetic capacity induced leaf senescence (Grbić and Bleecker 1995), sucrose content in leafy spurge leaves increased to levels as high as that during the beginning of the growing season. The most likely explanation is that sugar was being mobilized during leaf senescence for translocation to roots and underground adventitious buds for acclimation and over-winter survival. This would explain the sharp increase in bud TNC observed during this same period (Figure 2B). Accumulation of sugars and other solutes is often correlated with cold acclimation among plant species that survive freezing temperatures (Levitt 1980), although there are exceptions (Graham and Patterson 1982). Also, short day length and low temperature are environmental cues known to trigger cold acclimation in freeze-tolerant plants (Welling et al. 2002), both of which were declining throughout August to October (Figures 1 and 3) in the present study.

Furthermore, between August and October, during para-dormancy and transition into endodormancy, Anderson et al. (2005) previously showed that there is a distinct up-regulation of hexokinase and sucrose synthase gene expression in leafy spurge underground adventitious buds. This enhanced gene expression indicates an influx of sugar and further supports our postulate that carbohydrates are exported from leaves to buds during this time.

It is also during late August through October that there is a steep rate in swelling and expansion of leafy spurge adventitious buds (Anderson et al. 2005), which coincides with a transition from para- to endodormancy (Anderson et al. 2005; Chao et al. 2006). Soluble sugars, particularly sucrose and glucose, have been suggested to play a vital role in signaling the transition to innate dormancy (endodormancy) of adventitious buds during autumn (Anderson et al. 2005). This likely plays a role in preventing new shoot growth, because temperatures during this period are still conducive to growth. This is important because endodormancy bridges the gap between the loss of paradormancy and the induction of ecodormancy in underground adventitious buds. Results from the present study suggest that the soluble sugar providing this signal likely result from conversion of starch reserves in leaves to sucrose during senescence for remobilization to roots and underground adventitious buds during late summer and autumn.

Conclusions

Results of this study have shown that photosynthesis and overall carbohydrate accumulation were greatest during early development of leafy spurge plants. Photosynthate partitioning in leaves favored starch accumulation in early to mid-summer followed by remobilization to sucrose in late summer and autumn. Subsequent translocation of leaf sucrose is likely key to providing the carbohydrate for growth and development of underground adventitious buds as well as potentially providing a sugar-mediated signal for conferring innate dormancy status.

Gaining a better overall understanding of carbohydrate flux and partitioning in leafy spurge plants, including the involvement of sugars in regulating underground adventitious bud development and well-defined phases of dormancy, should provide insights for devising better biological and integrated pest management strategies for controlling leafy spurge infestations. Transgenic approaches have been used for some plant species to manipulate photosynthetic carbon flow and to study the partitioning between source and sink tissues (Galtier et al. 1995; Hattenbach et al. 1997; Signora et al. 1998). For future research, these approaches may lend themselves well for studying modifications of carbohydrate source–sink balance and sugar signaling in leafy spurge. Diversion of photosynthate away from starch storage in leafy spurge leaves in early and mid-summer could be envisioned to disrupt the flux of carbohydrates to underground adventitious buds during para- and endodormancy that occur in late summer and autumn. If sugars are involved in regulating bud dormancy as previous evidence indicates (Anderson et al. 2005; Chao et al. 2006; Horvath 1999), then disrupting carbohydrate flux to underground adventitious buds, or blocking the sensing and signaling pathway, could potentially break dormancy or weaken bud development and disrupt growth during the subsequent year.

Sources of Materials

[1] LI-6400 Portable Photosynthesis System, LI-COR, 4421 Superior Street, Lincoln, NE 68504.

[2] 0.45 μm, Whatman Inc., 200 Park Ave., Suite 210, Florham Park, NJ 07932.

[3] HPLC, Agilent Technologies, 363 Vintage Park Drive, Foster City, CA 94404.

[4] Aminex HPX-87N column, Bio-Rad Laboratories, 1000 Alfred Nobel Drive, Hercules, CA 94547.

[5] Amyloglucosidase, Roche Diagnostic Corp., P.O. Box 50414, 9115 Hague Road, Indianapolis, IN 46250.

[6] TableCurve 2D, version 5.0, SYSTAT Software, Inc., 1735 Technology Drive, Suite 430, San Jose, CA 95110.

[7] SAS PC Windows, version 9.1.3, SAS Institute, Inc., 100 SAS Campus Drive, Cary, NC 27513.

Acknowledgments

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